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Retention of solute and particle markers in the digestive tract of chinchillas (*Chinchilla laniger*)

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Running head: Chinchilla digesta kinetics

Abstract

The chinchilla (*Chinchilla laniger*) is a herbivorous hystricomorph South American rodent for which no mean digesta retention times have been reported so far. Six animals (mean body mass ± standard deviation: 513 ± 99 g) on a diet of grass hay and lucerne-based pellets were given a pulse dose of a solute (cobalt-EDTA) and a particle (chromium-mordanted fibre, <2mm) marker with subsequent frequent faecal collection. Dry matter intake was 45.2 ± 8.0 g/kg$^{0.75}$/day. Mean retention times were 22.2 ± 5.3 h for solutes and 25.4 ± 5.2 h for particles, with the difference being not significant within individuals. This indicates the presence of a 'mucus trap' colonic separation mechanism, which is in accord with morphological descriptions of the typical colonic furrow in chinchillas. Corresponding to a strategy of colonic digesta separation and caecotroph formation, secondary marker excretion peaks indicated coprophagic events that were spaced approximately 12 h apart. Given that these retention times appear longer than measures reported for rabbits (*Oryctolagus cuniculus*) or guinea pigs (*Cavia procellus*), it would be interesting to compare the digestive efficiency of chinchillas on high levels of dietary fibre to other species.

Key words: chinchilla, digestion, coprophagy, caecotrophy, herbivory, fermentation

Introduction

Coprophagy is a digestive strategy employed by small herbivores to reduce potential losses of nutrients associated with the shedding of microbial matter, originating from hindgut fermentation, with the faeces (Karasov and Martínez del Rio 2007). In order for this strategy to be efficient, the material excreted as faeces has to be separated into the part that is foreseen for re-ingestion, and the part that is definitely excreted. The mechanism that secures this separation has been termed 'colonic separation mechanism' (CSM, Björnhag 1972). Two fundamentally different CSM have been documented (Hume and Sakaguchi 1991; Björnhag and Snipes 1999; Franz et al. 2011). The one present in lagomorphs (rabbits and hares) is linked to a retrograde digesta washing in the colon that flushes bacteria back into the caecum, and is called the 'wash back' CSM. The one present in rodents, called 'mucus trap' CSM, is based on the extraction of microbes from the digesta into mucus contained in a specific colonic structure, in which the trapped microbes are transported back to the caecum. In hystricomorph ('porcupine-like', including guinea pigs *Cavia porcellus* or chinchillas) rodents, this specific structure is the so-called colonic 'furrow' (Gorgas 1966; Snipes et al. 1988) and has been studied extensively (Takahashi and Sakaguchi 2000; 2006). In myomorph ('mouse-like') rodents, the mechanism might be linked to certain longitudinal folds and oblique furrows (*Plicae circulares*) in the colon (Behmann 1973; Sperber et al. 1983) but has not been investigated in detail. From the caecum, the material separated by the CSM is excreted as caecotrophs, re-ingested by the animal, and subject to enzymatic digestion in the stomach and the small intestine. The corresponding mechanism in shrews, which also practice coprophagy (Loxton et al. 1975), has not been identified.

Digesta passage experiments, in which an indigestible marker is ingested as a pulse-dose by the animals, and its concentration subsequently documented in faeces over time, can demonstrate coprophagic behaviour *per se* due to secondary marker peaks indicating repeated marker uptake from the faeces (Clauss et al. 2007). Secondary peaks do not necessarily occur,

because reingestion of microbial components may not be required if the diet itself offers nutrients, in particular protein, in high concentrations. Thus, coprophagy was shown to vary with diet in rabbits (*Oryctolagus cuniculus*) (Fekete and Bokori 1985; García et al. 1995) or viscachas (*Lagostomus maximus*) (Hagen et al. 2015a). Passage experiments can further differentiate between the 'wash back' CSM, in which solute markers are particularly recycled via coprophagy and hence have much longer retention times than particle markers, and the 'mucus trap' CSM in which solute and particle markers move together (Hume and Sakaguchi 1991; Pei et al. 2001; Franz et al. 2011).

Chinchillas (*Chinchilla laniger*) are herbivorous South American rodents. Their natural diet mainly consists of grasses but also herbs, barks of bushes, bromeliads or fruits of cactuses, depending on the availability of the respective plants (Cortés et al. 2002). Chinchillas have a long history of being kept both as fur animals and as pets. Feeding recommendations include the provision of a roughage source, high-fibre pellets and only limited amounts of fresh vegetation or vegetables (Wolf et al. 2003; Grant 2014; Kohles 2014). Chinchillas have a colonic furrow typical for hystricomorph rodents (Gorgas 1966) that is an integral part of their 'mucus-trap' CSM (Holtenius and Björnhag 1985). Without indicating source or method, Johnson-Delaney (2006) states that the transit time of digesta through the gastrointestinal tract of chinchillas is 12-15 h. An estimation for a mean digesta retention time has been reported as 35 h in a study with food withdrawal, continuous marker application for 24 h and long faecal sampling intervals (Krishnamurti et al. 1974), but so far, the excretion patterns and mean retention times (MRT) for solute and particle markers have not been investigated in this species. Such data is of special interest because, compared to other hystricomorph rodents, chinchillas have a particularly long large intestine (Gorgas 1966). This may represent an adaptation to arid habitats and may allow them to live on lower water intakes than other rodents (Hagen et al. 2014). We hypothesized that passage marker excretion patterns would indicate coprophagy by secondary peaks, a 'mucus trap' CSM by

parallel movement of solute and particle markers, and yield long MRT values due to the long colon in this species.

Material and Methods

Six chinchillas (*Chinchilla laniger*; mean body mass ± standard deviation: 513 ± 99 g) were used before in a study on food and water intake (Hagen et al., 2014) (experiment licence 80/2012). The animals were housed individually in open boxes with wood shavings in a room with temperature ranging between 22 and 26 °C. The chinchillas were fed grass hay (g/kg dry matter: crude protein, 221; neutral detergent fibre (NDF), 588) and commercial, lucerne-based pellets (g/kg dry matter: crude protein, 139; NDF, 369) ad libitum. Food intake was quantified by weighing the amount of diet items offered and weighing leftovers at the next feeding. The MRT of a solute marker (cobalt-EDTA) and a particle marker (chromium-mordanted fibre particles <2mm), prepared according to Udén et al. (1980), were measured. Chromium concentration in the mordanted fibre was 37 g/kg dry matter. Markers were fed in quantities of 0.01 g Co-EDTA and 0.04 g mordanted fibre per animal as a pulse-dose at 18:00 hrs, mixed with a hay-based diet formula (Critical CareOxbow Animal Health, Murdock NE) and administered orally with a syringe in manually restrained animals (taken out of their enclosure). Care was taken to wipe off all non-ingested marker mix from the animals' snouts, and to avoid carry-over of marker mix into the enclosure when placing the animals back. Sampling of faeces was performed every 4 h during the first 48 h, every 6 h the next 48 h, and once on day 5. Faeces were analysed for markers after wet ashing by atomic absorption spectroscopy according to Behrend et al. (2004). Samples that deviated from the general pattern of a decreasing marker concentration after an initial peak (i.e., samples later interpreted as 'secondary peaks') were analysed in duplicate if sufficient amounts were available. The MRT through the whole digestive tract were calculated according to Thielemans et al. (1978) as

$$MRT = \frac{\Sigma\, t_i\, C_i\, dt_i}{\Sigma\, C_i\, dt_i}$$

with C_i = marker concentration in the fecal samples from the interval represented by time t_i (h after marker administration, using the midpoint of the sampling interval) and dt_i = the interval (h) of the respective sample

$$dt_i = \frac{(t_{i+1}-t_i)+(t_i-t_{i-1})}{2}$$

The marker was assumed to have been excreted completely once the fecal marker concentrations were similar to the background-levels determined in pre-dose fecal samples. The MRT for the two markers were normally distributed and compared by paired t-test using SPSS 21.0 (SPSS Inc. Chicago, IL).

Results

The relative average dry matter intake (per unit metabolic body weight) was 45.2 ± 8.1 (range 34-55) g/kg$^{0.75}$/day. Transit time (time of first marker appearance in faeces) was as short as 4 h in some individuals, and 8 or 12 h in the others (Fig. 1). The mean MRT for the solute marker (Co) was 22.2 ± 5.3 (range 16.3-30.2) h, and that of the particle marker (Cr) 25.4 ± 5.2 (range 19.5-34.1) h. The excretion patterns were characterised by 2 to 4 marker peaks (Fig. 1) that were sometimes only 12 h apart, in particular the first and the second peak. The two markers moved mostly in parallel. The difference between them was not significant at the 0.05 level even though a trend for a longer particle retention was apparent (P = 0.082). This was most likely due to two animals in which the majority of the particle marker was only excreted after the first coprophagic event (Fig. 1c and f).

Discussion

The results confirm that the chinchilla has a 'mucus-trap' CSM and practices coprophagy, a behaviour that is difficult to observe directly. With respect to the exact magnitude of digesta retention times in chinchillas, additional experiments using a variety of diets and intake levels are warranted. With respect to the markers used, it should be tested whether mordanted fibres are really representative for indigestible digesta in rodents, even if the widespread use of these markers facilitates the inclusion of the results of the present study in larger datasets (e.g. Müller et al. 2013). In particular, the identification of secondary marker peaks could be a bone of contention, because one could debate whether certain peaks are simply individual artefacts or truly represent coprophagy events. Care to avoid enclosure contamination with passage markers during marker application, and repeating analyses for critical samples, as both done in this study, can increase the interpretation safety only to a certain extent. Especially with respect to suggested secondary peaks with greater distance to the time of marker application, as e.g. marked in Fig. 1a, 1e or 1f, it would be beneficial to maintain the more frequent and labour-intensive faecal sampling regime that is typically only applied during the first two days in passage studies. Events that are not only indicated by a single peaking value, but by several samples indicating a recurrent increase and decrease in marker concentration (as e.g. evident in the first peaks in Fig. 1e), could more reliably be interpreted as non-artefacts. However, it must be noted that recurrent marker peaks have also been documented in individuals of species that are not known for coprophagy, where contamination of faeces with marker substrate could be excluded, and where no reingestion of faeces were observed during the experiment (e.g. Matsuda et al. 2015). Therefore, marker excretion patterns should always be considered in the context of other morphological and physiological data.

Given the variation in whether similar or dissimilar concentrations of both markers were excreted at secondary peaks, it must be concluded that the 'mucus-trap' CSM shows no clear preference for either the solute or the particle marker, and that possibly a degree of chance is

involved with respect to the degree a marker is retained. The spacing of the repeated marker excretion peaks suggests a rhythm of coprophagy that is shorter than 24 h and closer to 12 h. This matches the findings of Holtenius and Björnhag (1985) who observed single coprophagy events in chinchillas during the whole day (but not during the night). Similarly, the distance between marker excretion peaks in viscachas suggested coprophagy events at 12 h time intervals (Clauss et al. 2007). Also, some distances between marker excretion peaks in rabbits and guinea pigs were of similar magnitude (Sakaguchi et al. 1987; Franz et al. 2011). However, in rabbits, marker peaks spaced 24 h apart have also been reported (Sakaguchi et al. 1987). Apparently, the rhythm of coprophagic events varies between species. Some rodents practice coprophagy multiple times during the day, such as the herbivorous vole (*Microtus californicus*) (Kenagy and Hoyt 1979), the meadow vole (*M. pennsylvanicus*) (Ouellette and Heisinger 1980), the Norway lemming (*Lemmus lemmus*) (Björnhag 1977) or the mountain beaver (*Aplodontia rufa*) (Ingles 1961). The degu (*Octodon degu*) is another animal that practices coprophagy about every 12 h, but in contrast to the chinchilla, the degu shows this behaviour only at night (Kenagy et al. 1999). In mountain hares (*Lepus timidus*) (Pehrson 1983), kangaroo rats (*Dipodomys microps*) (Kenagy and Hoyt 1979), nutrias (*Myocastor coypus*) (Gosling 1979) and capybaras (*Hydrochoerus hydrochaeris*) (Herrera 1985), a rhythm of 24 h for coprophagy was observed. Apart from these apparent species differences, variation in the nutrient composition and the amount of the available diet may change coprophagic behaviour within species (Fekete and Bokori 1985; García et al. 1995; Kenagy et al. 1999; Hagen et al. 2015a).

In contrast to MRTs in rabbits (app. 15 h) and guinea pigs (app. 18 h) with the same passage markers on a grass hay-only diet (Franz et al. 2011), chinchillas appear to achieve surprisingly long MRTs for their body size, reaching values in the lower range of horses on a grass hay-only diet with the same marker system (23-34 h, Clauss et al. 2014). Whether this translates into higher fibre digestibilities in chinchillas than for example in rabbits and guinea

pigs or is simply a side effect of the fact that chinchillas have, for hystricomorph rodents, a particularly long large intestine for water re-absorption as an adaptation to their arid habitat (Gorgas, 1966), remains to be investigated. The few digestibility measurements that have been reported for chinchillas do not allow to conclusively decide whether the digestive efficiency of chinchillas is equally or less affected by dietary fibre compared to rabbits or guinea pigs (Hagen et al. 2015b). Reports that pet chinchillas suffer from body mass losses when kept on a diet of either grass hay or fresh grass alone (Wolf et al. 2003) apparently do not match a high fibre digestibility one would intuitively link with long retention times. Even though coprophagy is understood mainly as a mechanism to recycle nutrients related to gastrointestinal microbes (reviewed in Karasov and Martínez del Rio 2007; Franz et al. 2011), the fact that the fibre marker in the present study and similar studies is also recycled by this mechanism suggests that some fibrous components will also be submitted to a second, and hence prolonged, fermentation in the gastrointestinal tract of hindgut fermenters with a 'mucus trap' CSM.

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316 **Figure 1** Marker excretion patterns for a solute (cobalt-EDTA) and a particle marker
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318 study. Note the recurrent marker peaks (marked by arrows), indicative of coprophagy, and the
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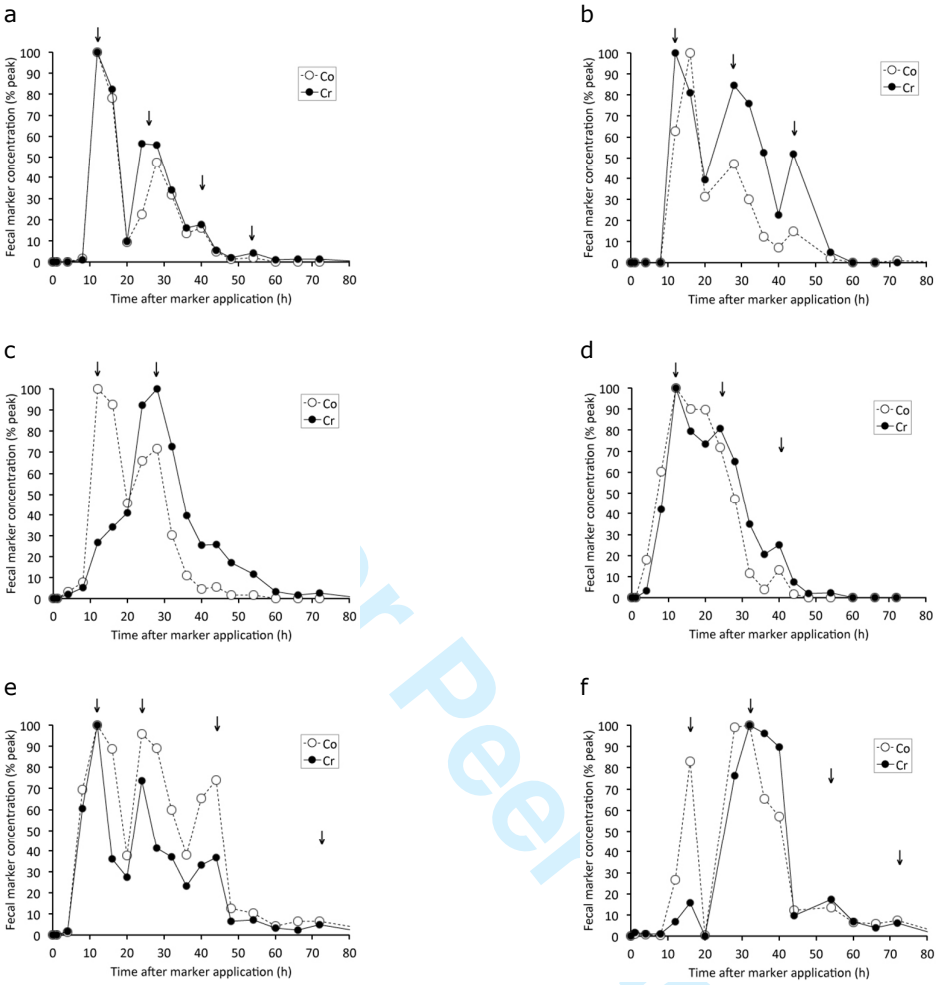
320



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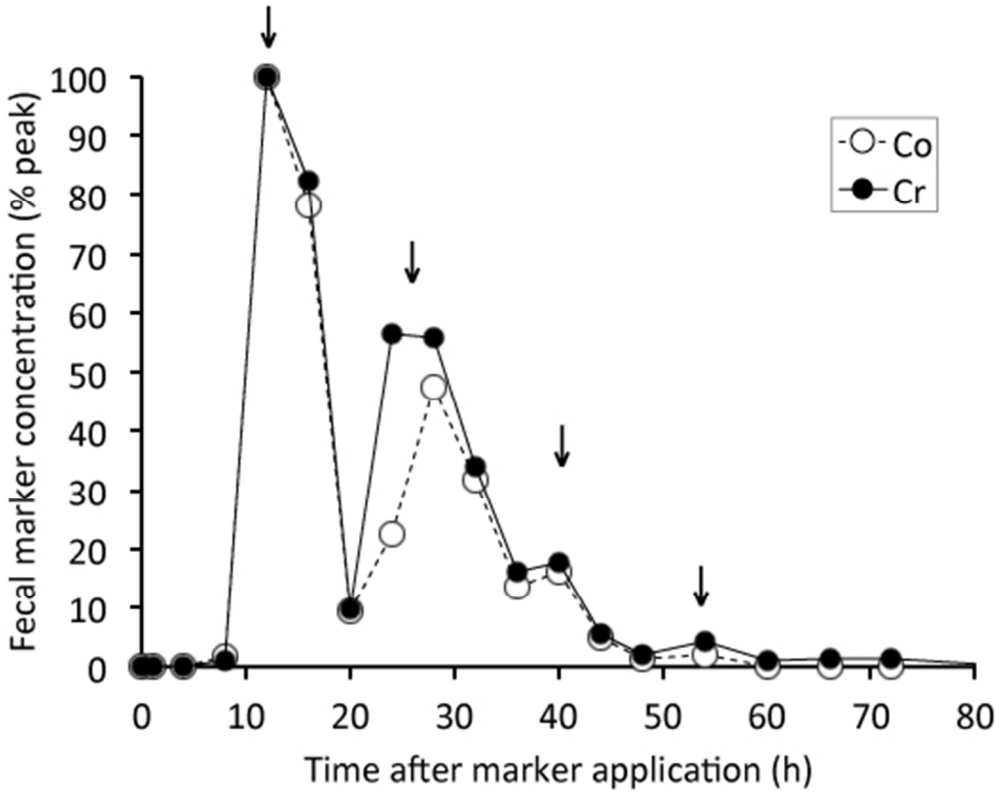

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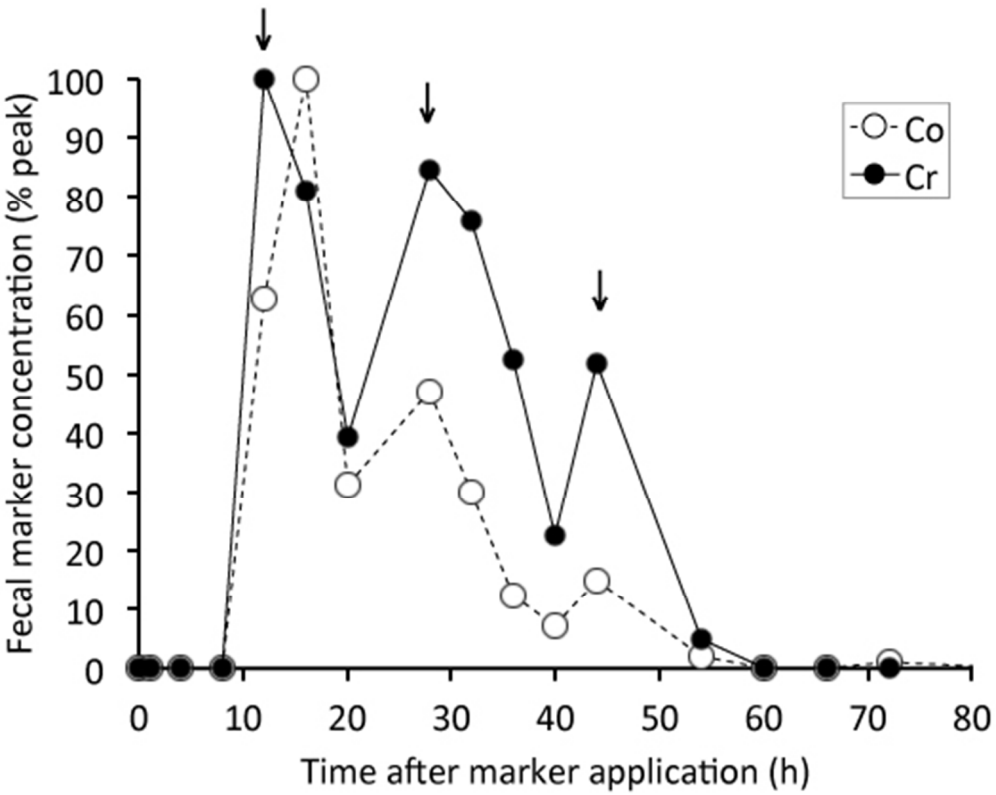

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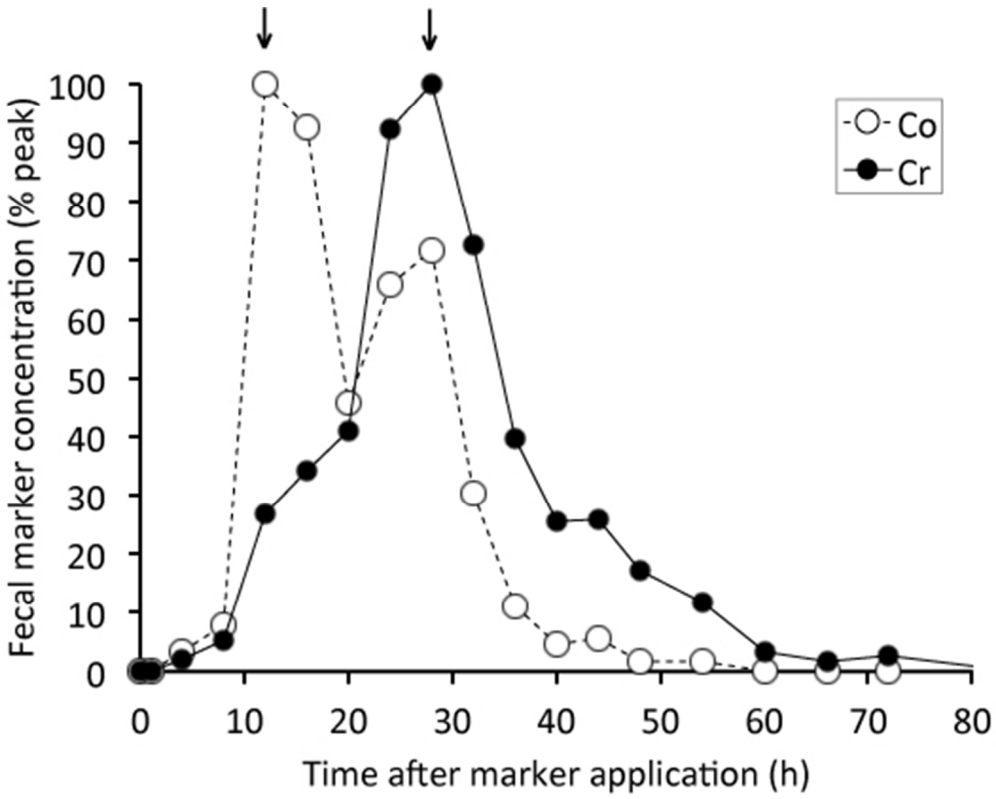


Figure 1 Marker excretion patterns for a solute (cobalt-EDTA) and a particle marker (chromium-mordanted fibre, < 2 mm) in the six chinchillas (Chinchilla laniger, a-e) of this study. Note the recurrent marker peaks (marked by arrows), indicative of coprophagy, and the general absence of difference in pattern between the two markers within individuals.
13436x10668mm (1 x 1 DPI)

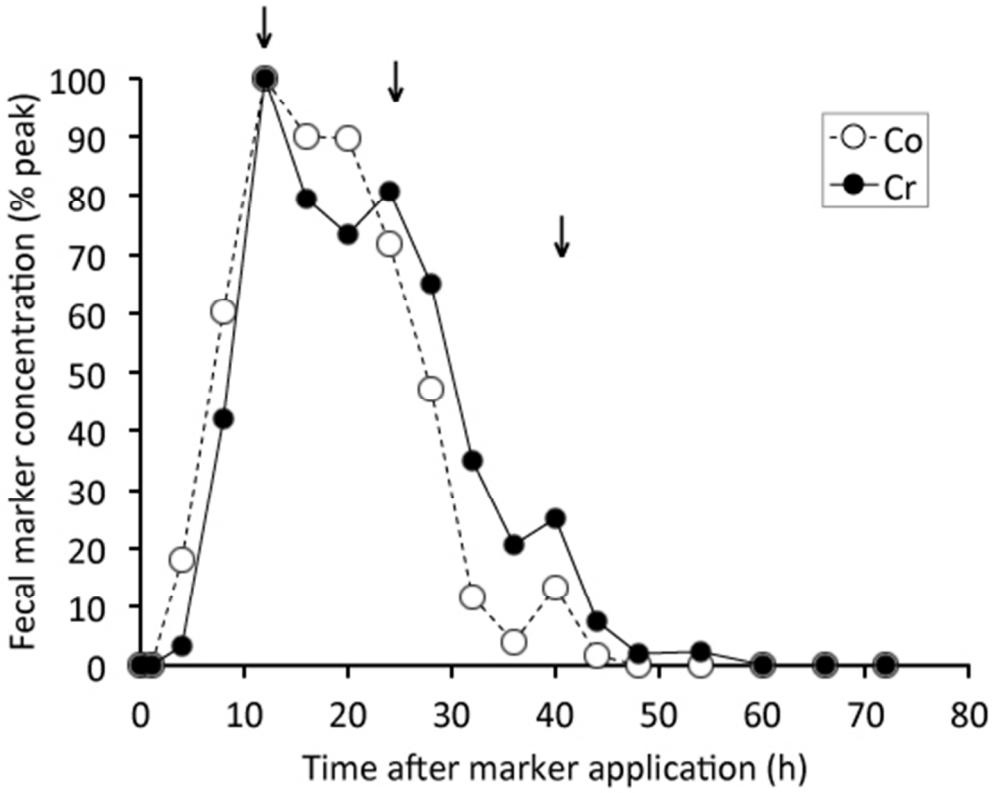
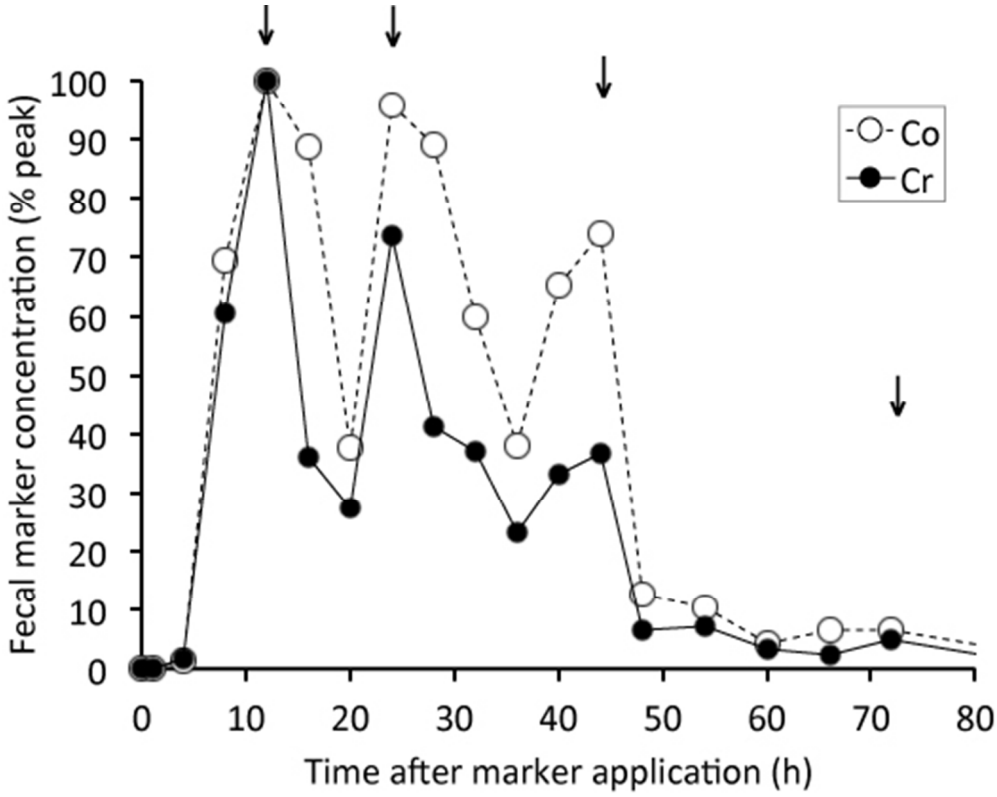


Figure 1 Marker excretion patterns for a solute (cobalt-EDTA) and a particle marker (chromium-mordanted fibre, < 2 mm) in the six chinchillas (Chinchilla laniger, a-e) of this study. Note the recurrent marker peaks (marked by arrows), indicative of coprophagy, and the general absence of difference in pattern between the two markers within individuals.
13487x10668mm (1 x 1 DPI)



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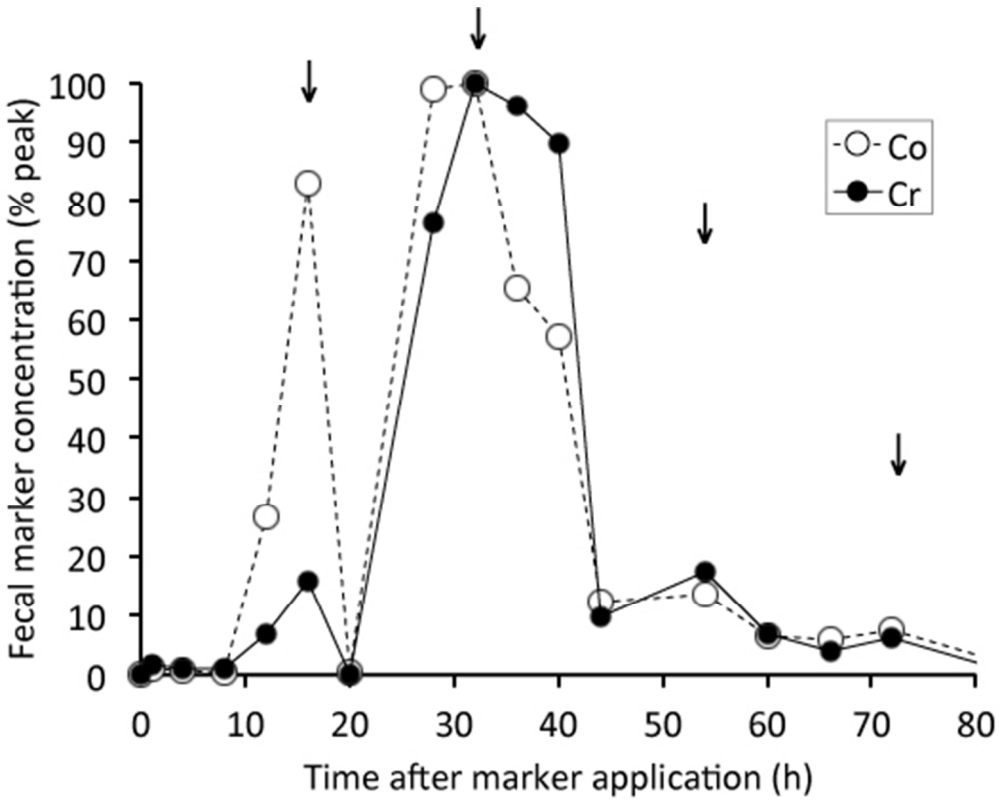
13411x10617mm (1 x 1 DPI)



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13385x10642mm (1 x 1 DPI)